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The ghost fruits of Madagascar: Identifying dysfunctional seed dispersal in Madagascar's endemic flora

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ABSTRACT

Madagascar lost a large number of large-bodied animal species during the Holocene. Many of them played important roles as seed dispersers. In the case of the largest-seeded species, giant lemurs or elephant birds may have been the sole dispersers because no extant frugivore has a gape size large enough to ingest those seeds. These plant species now show all the hallmarks of anachronistic species. The consequences of dispersal gaps caused by megafaunal extinctions are exacerbated by the continuing decline of the range distribution of extant dispersers, particularly lemurs. In this paper, we identify dispersal gaps in Madagascar and highlight dysfunctional seed dispersal – systems in which plants have lost animal mutualists. We obtained data on seed dispersal, traits and distribution of plants and frugivores in Madagascar from the literature, online databases, and using herbarium specimens. We estimated the number of potential dispersers for each endemic endozoochorous plant species, by comparing the seed size of each plant species to the size of the largest seed that each frugivore can swallow whole. We estimated the number of available lemur dispersers by matching the distribution of plant species to the distribution of potential dispersers. We found that, out of the 3018 studied endozoochorous plant species, two species have experienced the complete extinction of their main dispersers while 487 species suffer from the local extinction of their suitable dispersers. A limited number of dispersers could be one of the main reasons why most of these plant species are now on the edge of extinction.

1. Introduction

Globally, a majority of Angiosperms rely on animals for seed dispersal ("zoochory") (Howe and Smallwood, 1982). Unfortunately, zoochorous species are more vulnerable to anthropogenic disturbances than abiotically dispersed plant species, because their disperser populations are often strongly impacted by such disturbances (Pérez-Méndez et al., 2016). Large-seeded plant species are often the most vulnerable because they rely on a restricted number of large-bodied frugivores that are more sensitive to habitat disturbance (Cramer et al., 2007; Galetti and Dirzo, 2013; Pérez-Méndez et al., 2016). Although a slow process, the loss of animal seed dispersers has been shown to considerably increase the risk of extinction for zoochorous plants (Caughlin et al., 2014; Chapman and Chapman, 1995; Muller-Landau, 2007; Razafindratsima and Dunham, 2015).

Madagascar is one of the most threatened biodiversity hotspots on Earth (Myers et al., 2000). Levels of endemism are extreme, reaching up to 82% in vascular plants (Callmander et al., 2011) and 84% in vertebrates (Goodman and Benstead, 2005). One exceptional aspect of Madagascar's biodiversity is that, compared to other tropical areas, it always had a strikingly small proportion of frugivorous and, therefore, seed-dispersing animals (Godfrey et al., 2008; Goodman and Ganzhorn, 1997). In most systems worldwide, birds and mammals are the most important seed dispersers (Howe and Smallwood, 1982). However, Madagascar's avifauna has few frugivorous taxa, with only 12 species that can be considered as seed dispersers rather than seed predators

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(Table A1). On the other hand, of the 101 extant lemur species (Schwitzer et al., 2014), Madagascar's unique primates, 25 are frugivores and consequently potential seed dispersers. Therefore, lemurs are by far the most dominant seed dispersers in this biodiversity hotspot, to the point that they have even shaped some plant communities (Buerki et al., 2015; Génin and Rambeloarivony, 2018; Razafindratsima and Dunham, 2016). However, alarmingly, 94% of all lemur species are currently threatened with extinction mainly due to habitat loss and hunting (IUCN, 2019). This dramatic loss of animal species in Madagascar began ~2000 years ago, and is biased towards large-bodied animals (Burney et al., 2004; Crowley, 2010). At least 48 species of large (> 10 kg) mammals, birds and reptiles were driven to extinction (Burney, 1993; Godfrey and Jungers, 2003a; Mittermeier et al., 2010). Many of the extinct giant lemurs (e.g. *Pachylemur* spp. and *Archaeolemur* spp.), elephant-birds (*Aepyornis* spp. and *Mullerornis* spp.) and giant tortoises (*Aldabrachelys abrupta* and *A. grandidieri*) probably had a diet of fruits or a mixed diet of fruits and leaves, and could have been seed dispersers (Burney et al., 2004; Godfrey and Jungers, 2003b; Godfrey et al., 2008; Goodman and Jungers, 2014) (Table A2). With the disappearance of the island's megafauna, the animals' mutualist plant partners have become orphans, displaying their anachronism through strikingly unfit patterns, limiting or even preventing their seed dispersal by the extant fauna (Guimarães Jr. et al., 2008; Janzen and Martin, 1982). In addition, most extant dispersers have suffered from a drastic decrease of their populations and distribution ranges (Godfrey et al., 1997; Godfrey et al., 1999; Hawkins and Goodman, 2003; Schwitzer et al., 2013) leaving many zoochorous plant species without a disperser.

Given the complete extinction of Madagascar's megafaunal dispersers and the continuing decline of extant lemur populations leading to local extinctions, many plant species have undoubtedly been left with so few dispersers that the dispersal of their seeds is reduced or disrupted. A scientific investigation into which of the island's unique plant species are prone to dysfunctional dispersal is therefore urgent for conservation of plants lacking effective seed dispersers. In this study, we focus on lemurs as they are larger-gaped than birds and bats (Bollen et al., 2004; Dew and Wright, 1998), and thus represent the upper limit of seed sizes that can theoretically be dispersed by extant frugivores. We provide empirical evidence to support the hypothesis that a number of plant species suffer from dysfunctional seed dispersal due to (a) the complete extinction of their main dispersers, highlighted by a mismatch between seed size and maximum ingestible food size of extant dispersers, and (b) the local extinction of extant dispersers, highlighted by the mismatch between the distributions of plants and their respective potential dispersers.

2. Material & methods

2.1. Data collection

To gather data on traits (fruit type, diaspore colour, thickness of fruit husk, pulp type, fruit length and width, and seed length and width) and distribution of endemic Malagasy plant species, we reviewed the literature (botanical descriptions) and databases (Madagascar Catalogue, 2013), and examined fruit and seed specimens at the Royal Botanic Gardens, Kew (2519 specimens of 1148 species) and, when not available, at the Muséum National d'Histoire Naturelle, Paris (364 specimens of 278 species). We also performed a literature review to gather data on animals' traits (size, diet, habitat and distribution; Table A1) and on seed dispersal in Madagascar (Table A3).

2.2. Imputation of missing data in the plant trait dataset

With Madagascar's seed dispersal ecology still only poorly researched, our dataset of plant traits relevant for seed dispersal inevitably contained many gaps. Due to the random scattering of missing values across the dataset, a complete case analysis, in which all observations with one or more missing values were omitted, would include only 281 plant species (i.e. just 3% of the original 8788 species) (Albert-Daviaud et al., 2018) and would have led to non-negligible loss of power with misleading results and biased estimates of parameters (Ambler et al., 2007; Giorgi et al., 2008). We therefore decided to perform multiple imputations of missing values (Rubin, 1987) by using multivariate imputations by chained equations (MICE) (van Buuren and Groothuis-Oudshoorn, 2011). The algorithm generated 20 imputed datasets to capture most of the uncertainty underlying the imputation process (Bodner, 2008; Graham et al., 2007; White et al., 2010). Then, we analysed each imputed dataset individually and identically, and pooled the estimates from each dataset to obtain the final result (Rubin, 1987). We used the packages 'mice' and 'miceadds' in R v. 3.0.1 (R Development Core Team, 2013). The methods have been described in detail in Albert-Daviaud et al. (2018) and the corresponding scripts are available from the first author upon request.

2.3. Seed dispersal syndromes

We defined the seed dispersal syndromes of each species based on morphological traits of fruits and seeds. We first defined endozoochorous species based on the presence of edible rewards such as fruit pulp or aril (van der Pijl, 1982). We found 3324 species of endozoochorous plants, which represented 38% of the endemic Malagasy flora (N = 8784 species). Subsequently, where possible, we assigned either the primate-dispersal syndrome or the bird-dispersal syndrome to each endozoochorous species, based on diaspore colour and thickness of the fruit husk. The methods have been described in detail in Albert-Daviaud et al. (2018).

2.4. Identifying species missing their extinct dispersers (i.e. anachronistic species)

A mismatch between disperser gape size and seed size is the most obvious indicator of dispersal anachronism in endozoochorous species. Therefore, in Madagascar, we considered a species anachronistic if it was endozoochorous and possessed seeds that were larger than the largest seed dispersed by any living native frugivores. Gape size of frugivores being the limiting factor, we based our decision on the second largest dimension of a seed, hereafter referred to as 'width'. We used the width of the largest seed known to be ingested as an indirect indicator of maximum gape size. Previous authors considered fruit size as one of the most important indicators of anachronism (Guimarães Jr. et al., 2008; Janzen and Martin, 1982). However, without direct observations, we focussed primarily on seed size. For successful endozoochory, seeds have to be swallowed whole to retain their viability. Therefore, seed width is a non-negotiable limiting factor ruling out endozoochory by any animals with insufficient gape size.

Dispersal observations were lacking for some lemur species. In these cases, we estimated the width of the largest seed dispersed. The maximum ingestible food size in lemurs is known to be linked to their body mass (Perry and Hartstone-Rose, 2010). Therefore, we fitted a linear model with the width of the largest seed (Vb) ingested by each frugivore (with dispersal observations) as a dependent variable and the body mass as an independent variable. We found a strong linear relationship between body mass and Vb ($F_{(1,11)}$ = 22.2, P = .0006) that we used to estimate the size of the largest seed potentially dispersed by the lemurs without dispersal observations (incl. Extant (Table A1) and extinct (Table A2) lemurs). We used R v. 3.0.1 (R Development Core Team, 2013).

The largest seeds known to be dispersed by extant lemurs are 38.50 mm wide (*Martellidendron karaka* by *Varecia rubra*; Razafindratsima, 2009; Razafindratsima and Martinez, 2012). The most likely conclusion is that species with larger seeds could only have been dispersed by the extinct megafauna. Using a linear model, we estimated that the largest seed that extinct giant lemurs are able to ingest was

Table 1
Anachronistic Malagasy plant species. *Imputed data.

Species	Family	Life form	Fruit type	Diaspore colour	Fruit epicarp thickness	Syndrome	Seed Width (mm)	Conservation status
Borassus madagascariensis	Arecaceae	Tree	Drupe	Yellow	Thick*	Primate	67.50	EN
Erythrina hazomboay	Fabaceae	Shrub	Legume	Contrast	No	Bird	12.00	VU

42.4 mm wide (*Palaeopropithecus ingens*; Table A2).

The largest seeds found to be dispersed by birds in Madagascar measured 11.88 mm wide (*Commiphora guillaumini* by *Coracopsis nigra*, *Dicrurus forficatus* and *Hypsipetes madagascariensis*; Bleher and Böhning-Gaese, 2000; Bleher and Böhning-Gaese, 2001). Bird-dispersed species with larger seeds could have been adapted to be dispersed by elephant birds (*Aepyornis* spp. and *Mullerornis* spp.).

As a logical consequence of gape-size limitation, the number of potential dispersers for a particular plant species decreases as seed size increases. In extreme cases, only large lemur species, the largest of which are now extinct, would be capable of swallowing the seeds. Therefore, we defined as "anachronistic" any plant species in Madagascar that had animal-dispersed fruits with seeds larger than 38.50 mm in diameter. For species only dispersed by birds (e.g. mimetic seeds) we exceptionally decreased the threshold to 11.88 mm. In addition, we highlighted obviously "overbuilt" fruits by recording any endozoochorous species with fruits larger than 100 mm width.

2.5. Identifying species lacking extant lemur dispersers due to local extinctions

Our aim was to analyse the co-occurrence of endozoochorous plants and frugivorous lemurs by comparing the current geographical distribution of both plants and lemurs (Fig. A1). We downloaded geographical distribution data of plant species on http://www.gbif.org/ (GBIF, 2017) and the vegetation map on http://www.vegmad.org/datasets_gis.html (Moat and Smith, 2007). We used the distribution of lemurs published by Goodman (1994) and IUCN (2019), except for *Cheirogaleus ravus* for which we did not find any published distribution. We have to note that occurrence data may be scarce and does not fully represent the distribution of some lemur species. First, we converted the distribution data of plants, lemurs and vegetation formations into rasters (i.e. grids of equally sized cells, each cell containing an attribute value and location coordinates) with 1 km × 1 km cells (hereafter, cells containing location points are called location cells). Then, we created a 5-km buffer around each location cell of lemurs to take into account potential movements around the recorded location. In other words, cells within 5 km of the lemur's location cell were converted into location cells. Because the largest lemurs (*Varecia* spp.) were known to have daily path lengths close to 3 km (Morland, 1993; Moses, 2010), we decided to use a conservative buffer of 5 km around the location of every lemur. Thus, we assumed that, when a plant species was within 5 km of a lemur's cell, it co-occurred with a given lemur species. The aim of this approach was to highlight plant species with the lowest probability of co-occurrence with lemurs. Then, to limit bias due to distribution data that could be artefacts or too old to represent the current distribution of lemurs and plants, we changed into non-location cells all location cells that did not fall into the vegetation formation the given species was known to be associated with. For example, *Tabernaemontana stellata* was associated with forests and bushlands, so we changed into non-location cells all location cells falling outside these two habitat types. Finally, we overlapped the raster of each lemur species to the raster of each plant species and analysed co-occurrence. For each plant species, we recorded the number of co-occurring frugivorous lemurs and the area of co-occurrence. Then, among these co-occurring lemurs, we recorded the number of potential dispersers (i.e. able to ingest the seed according to seed size). We used the functions 'raster', 'rasterize', 'clump', 'area' and 'mask' in the package 'raster' (Hijmans, 2016) in R (Document A1).

3. Results

Combining the published data from 36 studies with seed dispersal observations, we found that only 179 of the 3324 endozoochorous plant species (5%) have direct observations of seed dispersal by extant frugivores in Madagascar (Table A3).

3.1. Identifying species missing their extinct dispersers (i.e. anachronistic species)

Two plant species could be considered as anachronistic in Madagascar (based on dispersal syndrome and seed size; Table 1). Indeed, they did not have any potential disperser in any of the 20 imputed datasets. The seed widths of these species range from 12.0 mm (*Erythrina hazomboay,* Fabaceae) to 67.5 mm (*Borassus madagascariensis*, Arecaceae). *Erythrina hazomboay* bears mimetic black and red seeds (bird syndrome), whereas *B. madagascariensis* bears yellow drupes (primate syndrome) and produces both very large seeds (67.5 mm width) and very large fruits (165 mm width). Moreover, 12 endozoochorous species produce fruits from 100 to 165 mm width (Table 2). However, we should note that 86% of the endozoochorous plant species could potentially be dispersed by at least 15 species of lemurs (based on seed size only, without taking geographic distribution into account).

Table 2
Endemic endozoochorous species producing fruits that seemed "overbuilt" given the disperser assemblage found in Madagascar. *Imputed data.

Species	Family	Life form	Fruit type	Diaspore colour	Fruit epicarp thickness	Syndrome	Fruit width (mm)	Conservation status
Adansonia perrieri	Malvaceae	Tree	Berry	Brown	Thick	Primate	150.00	EN
Adansonia suarezensis	Malvaceae	Tree	Berry	Brown	Thick	Primate	140.00	EN
Adansonia za	Malvaceae	Tree	Berry	Brown	Thick	Primate	110.00	LR/nt
Borassus madagascariensis	Arecaceae	Tree	Drupe	Yellow	Thick*	Primate	165.00	EN
Brexia arborea	Celastraceae	Tree	Berry	Yellow*	Thick	Primate	100.00	NA
Hydnora esculenta	Hydnoraceae	LI	Capsule	Brown	Thick*	Primate	125.00	NA
Symphonia fasciculata	Clusiaceae	Tree	Berry	Brown	Thin	Primate	120.00	NA
Symphonia tanalensis	Clusiaceae	Tree	Berry	Grey	Thin	NA	150.00	NA
Tabernaemontana stellata	Apocynaceae	Tree	Follicarium	Contrast	No	Bird	100.00	NA
Treculia africana	Moraceae	Tree	Syncarp	Green	Thick	Primate	103.00	NA
Treculia lamiana	Moraceae	Tree	Syncarp	Green	Thick	Primate	300.00	NA
Treculia sambiranensis	Moraceae	Tree	Syncarp	Green	Thick	Primate	300.00	NA

3.2. Identifying species lacking extant lemur dispersers due to local extinctions

We performed spatial analyses on 3018 endozoochorous dispersed species for which GBIF had georeferenced records. More than half (51%) of this plant species co-occurred with five or fewer species of lemurs (Fig. A2; Table A4). As a result, we showed that 489 (16%) plant species did not have any available lemur disperser (i.e. potential disperser according to seed size which also co-occurs with the plant species) with an additional 747 species that had two or less available lemur dispersers. Each plant species had, on average, 4.3 available species of lemur dispersers. According to their seed size, 327 plant species could potentially be dispersed by at least 20 species of lemurs; but, due to their non-overlapping distribution, they did not have any disperser available (Table A4). On the other hand, two plant species co-occurring with nine and ten lemur species respectively could not be dispersed by any of them due to their seed size (Table A4).

4. Discussion

Although 38% of the endemic Malagasy species are clearly endozoochorous, only 179 of them have directly been observed to be dispersed by animals in Madagascar (Table A3). Additionally to a possible lack of observational data, it seems likely that lack of dispersers (due to local or complete extinction) is one of the main reasons that the dispersal by animals of > 3000 endozoochorous species has not been reported.

Our results suggested that at least 489 of Madagascar's endemic endozoochorous species suffer from dysfunctional dispersal due to disperser loss (488 species from lemur extinctions and at least one species from bird extinctions – *Erythrina hazomboay*). For two species, this was due to the complete extinction of their main dispersers, highlighted by the mismatch between seed size and maximum ingestible food size of extant dispersers. For at least 487 species, this was due to the local extinction of potential lemur dispersers. As a consequence of deforestation, habitat fragmentation and hunting, extant lemur populations have been massively reduced (Barrett and Ratsimbazafy, 2009; Schwitzer et al., 2014), and many species do not co-occur anymore with the plants whose seeds they could disperse.

4.1. Identifying species missing their extinct dispersers (i.e. anachronistic species)

As our study showed, several of the apparently undispersed pulpy species do possess seeds whose physical dimensions seem to exceed the maximum gape size of extant Malagasy frugivores (Table 1). There is a strong likelihood that the fruits of these species have evolved to be dispersed by extinct frugivores: at least six species could have been dispersed by giant lemurs (primate syndrome) whereas at least one species could have been dispersed by elephant birds (bird syndrome) (Table 2). The latter is *Erythrina hazomboay* (Fabaceae), which produces dehiscent fruits with large mimetic seeds (Foster and Delay, 1998). This is likely to represent an adaptation to dispersal by elephant birds. Displaying the hallmarks of the bird dispersal syndrome, the large and colourful mimetic seeds probably tricked these ratites into mistaking them for diaspores with fleshy rewards. Similar but smaller seeds have been described in numerous Fabaceae genera including three genera found in Madagascar (i.e. *Abrus*, *Adenanthera*, *Erythrina*; Du Puy et al., 2002; Foster and Delay, 1998; van der Pijl, 1982) (Fig. A3).

Several authors have already suspected that Madagascar's extinct megafauna played a significant role in the dispersal of various native plant species (Buerki et al., 2015; Godfrey et al., 2008; Goodman and Jungers, 2014). Moreover, some studies have demonstrated that the current large- and fine-scale distribution patterns of some Fabaceae species in Madagascar were best explained by their dispersal dependency on extinct species of the megafauna and their living relatives (Buerki et al., 2015; Devey et al., 2013).

Our study showed that, given their seed size, most anachronistic species could have been dispersed by the extinct giant lemurs, which strengthens our hypothesis. The only exception was *Borassus madagascariensis* (Arecaceae) whose seed width (67.5 mm) was well above the size of the largest seed that could potentially be dispersed by frugivorous giant lemurs (46.9 mm; *Palaeopropithecus maximus*). An African ancestor of the species had probably evolved to be dispersed by elephants (Baker and Couvreur, 2013; Burtt and Salisbury, 1929) and *B. madagascariensis* would have kept its morphological characteristics. Indeed, all *Borassus* species (in Africa and Asia) share the same characteristics (i.e. very large fleshy fibrous fruits with a coriaceous epicarp and very large seeds) (Bayton, 2007; Dransfield and Beentje, 1995). However, it raises the question of its survival on Madagascar. *Borassus madagascariensis* could have been dispersed by an even larger extinct frugivorous animal (lemur or not), not yet discovered, giant tortoises, or dispersed through barochory (Barot et al., 1999) or hydrochory (Dransfield and Beentje, 1995) before human or cattle could have played a role as seed dispersers. Indeed, populations are all in close proximity to human settlements (Bayton, 2007) and *B. madagascariensis* is used as a food resource for local people (palm-heart and fruit), although not cultivated (Dransfield and Beentje, 1995). Arecaceae was the most common family among anachronistic species, with three other species likely to display dysfunctional dispersal due to the size of their seeds: *Lemurophoenix halleuxii*, *Orania longisquama* and *Satranala decussilvae* (Table 1). Dransfield and Beentje (1995) hypothesized that *Satranala* fruits, with their highly sculptured endocarp, could have been adapted to be dispersed by elephant birds, and they witnessed an evidence of dysfunctional dispersal with fruits rotting in high number below the crown of adult trees.

Although we should treat anachronism as a continuum (Barlow, 2000), we decided to take a conservative approach by treating it as a binary concept (i.e. anachronistic or not). Indeed, it appeared too subjective to choose a number of extant dispersers below which we assumed a species was anachronistic. In Madagascar, the maximum number of dispersers is low compared to other areas. In this study, we decided to highlight the most anachronistic species, with no native disperser (i.e. extreme anachronism, following Barlow (2000)). However, it is important to note that 747 species had two or less available lemur dispersers (Table A4) and therefore they are also likely to suffer from dysfunctional seed dispersal. Three Fabaceae species (*Adenanthera mantaroa*, *Erythrina perrieri* and *Erythrina madagascariensis*), characterized by the production of mimetic seeds, could receive a particularly restricted dispersal service with only two potential disperser birds (*Alectroenas madagascariensis* and *Hypsipetes madagascariensis*).

4.2. Identifying species lacking extant lemur dispersers due to local extinctions

In addition to the extinction of some of the large dispersers, endozoochorous plant species have to face a further and probably even more important decrease of their disperser guild. Indeed, the range of the surviving dispersers has decreased so much (Godfrey et al., 1997; Godfrey et al., 1999) that their distribution does not overlap with that of the plant species whose seeds they would normally disperse (Table A4). This is the case for *Erythrophleum couminga* (Fabaceae) which could potentially be dispersed by seven lemur species (*Eulemur cinereiceps*, *E. collaris, E. flavifrons, E. fulvus, E. macaco, Varecia rubra* and *V. variegata*) according to the size of its seeds. However, none of these lemurs remains in the western coastal and subcoastal area where *E. couminga* is found (Fig. 1; Du Puy et al., 2002). In some cases, many lemur species co-occurred with a plant species but, given the size of its seeds, only a few of these lemurs were able to disperse it. *Canarium madagascariense* (Burseraceae) was a good example, co-occurring with 17 lemur species but potentially dispersed by only five of them (*Eulemur collaris, E. fulvus, E. macaco, Varecia rubra, V. variegata*) (Table A5). Among these species,

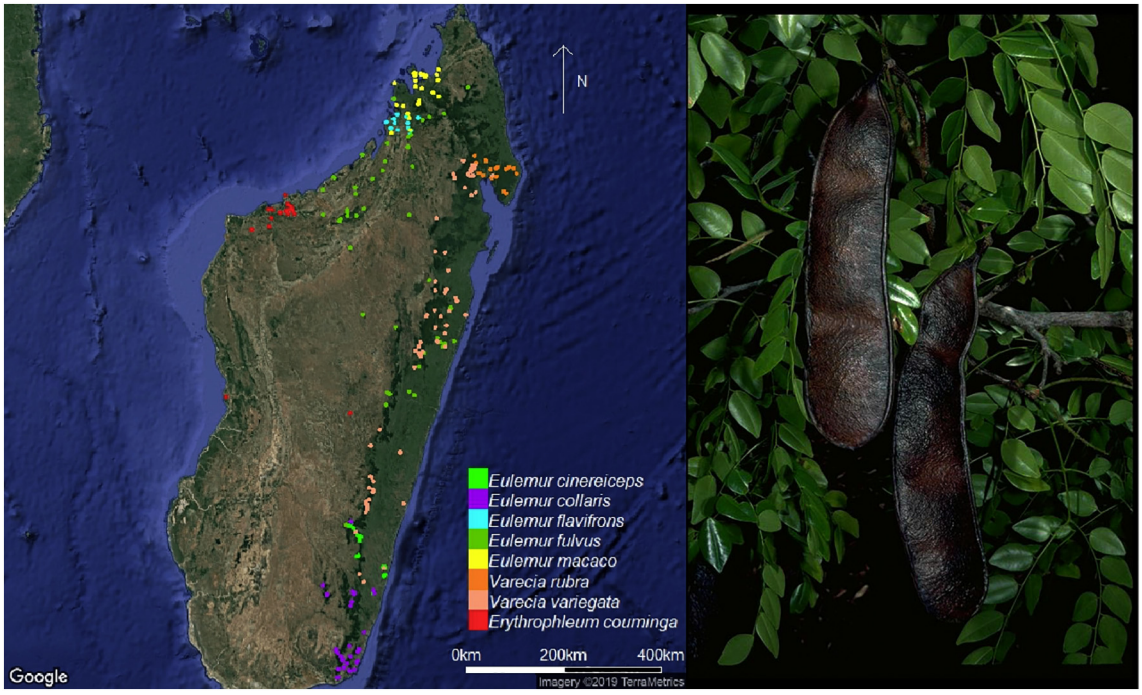

Fig. 1. Map showing the distribution of *Erythrophleum couminga* and the seven lemur species (*Eulemur cinereiceps*, *E. collaris, E. flavifrons, E. fulvus, E. macaco, Varecia rubra* and *V. variegata*) which could potentially disperse its seeds (based on seed size). Note that none of these lemur species still co-occurs with *Erythrophleum couminga*.

those bearing seeds < 11.88 m width could potentially be dispersed by some bird species.

It is important to note that the fast deforestation taking place in Madagascar quickly renders some occurrence data outdated. Therefore, we could have missed other plant species that are now lacking available dispersers. An example was *Eligmocarpus cynometroides* (Fabaceae). Our results showed that this species had five available lemur dispersers. However, the last update of its distribution reported only one persisting population with only 21 individuals (Devey et al., 2013). Given these data, *E. cynometroides* has only one remaining available disperser (*Lemur catta*: Fig. 2). It is confined to a very small area of south-east Madagascar, near a mining site and between villages, and shows clear evidence of disrupted dispersal, such as an absence of regeneration and large piles of rotten fruits below the trees (Buerki et al., 2015; Devey et al., 2013). *Eligmocarpus cynometroides* is now critically endangered.

Moreover, some species could display a large range of seed or fruit width (e.g. *Strongylodon madagascariensis* (Fabaceae, fruit width: 30–50 mm); *Dypsis heteromorpha* (Arecaceae, fruit width: 14–22 mm, seed width: 13–21 mm)). In these cases, for the ease of subsequent analyses, we estimated the midpoint of the range. However, the maximum width could be well above the average width and individuals producing the largest seeds or fruits could suffer from a dysfunctional seed dispersal more pronounced than estimated in this study.

Missing their primary dispersers, some species may experience limited or erratic dispersal by humans, livestock or rodents. In other parts of the world, rodents play an important role in the primary and/or secondary dispersal of large-seeded species (Jansen et al., 2012; Sánchez-Rojas et al., 2004; Wang and Chen, 2008). Whether these

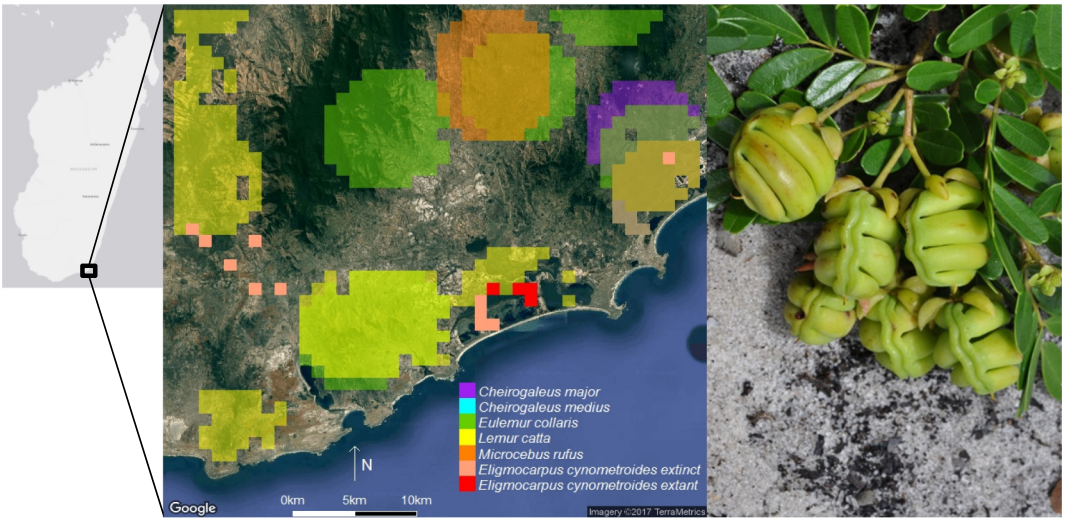

Fig. 2. Map showing the distribution of *Eligmocarpus cynometroides* (recently extinct and extant individuals) and the five lemur species (*Cheirogaleus major*, *C. medius, Eulemur collaris*, *Lemur catta* and *Microcebus rufus*) which could be able to disperse its seeds. Note that only one (*Lemur catta*) still co-occurs with *E. cynometroides*.

animals play a similar role in Madagascar is unknown because studies on seed dispersal by rodents on the island are lacking (but see Razafindratsima, 2017). However, observations of intact seeds of some plant species, such as *Cryptocarya* sp. (Lauraceae) and *Canarium* sp. (Burseraceae), in burrows of rodents have been reported on the island (Goodman, 1994; Goodman and Sterling, 1996; Razafindratsima, 2017). Moreover, we only took into account frugivorous lemurs in the analyses. However, some other lemurs, although predominantly acting as seed predator, may occasionally play the role of disperser but in a less efficient way (e.g. Propithecus edwardsi; Dew and Wright, 1998; Overdorff and Strait, 1998). Finally, in this study, we focused on lemurs because they are the most important dispersers in Madagascar. However, for small-seeded plant species lacking their lemur dispersers, birds and bats could play a key dispersal role, which needs to be further investigated.

4.3. Conclusions

A large part of endozoochorous species rely on lemurs for their dispersal (Albert-Daviaud et al., 2018). However, today, most lemur species are threatened with extinction due to habitat loss and forest fragmentation (Schwitzer et al., 2014), which strongly affects their role as seed dispersers (Bodin et al., 2006; Dausmann et al., 2008; Ganzhorn et al., 1999).

It has been demonstrated that the loss of animal seed dispersers considerably increases the risk of extinction for plants with endozoochorous seeds (Caughlin et al., 2014). So plant species with dysfunctional seed dispersal are probably on the edge of extinction. Out of the 111 endozoochorous plant species without any available lemur disperser and for which the conservation status has been assessed, 95% are already threatened with extinction, compared to 69% in the whole dataset ($N = 665$ species with conservation status). Moreover, 25% of the plant species without any available disperser are either already rare, with only one recorded location, or even known to be extinct in the wild (e.g. *Dypsis plurisecta*, Arecaceae), compared to 9% in the whole dataset ($N = 3018$ species). Although some Malagasy plant species lacking dispersers are presently still rather widespread (e.g. *Mammea sessiliflora* (Calophyllaceae)), these species may be suffering from dysfunctional seed dispersal, highlighting a potentially strong extinction debt. Today, the conservation status of 78% of Malagasy endozoochorous plant species is unknown (IUCN, 2019), which strongly limits the establishment of conservation plans. Evidence of dysfunctional seed dispersal such as those highlighted in our study could help to make a preliminary assessment of the most threatened species.

The findings from this and future studies on dysfunctional dispersal should directly influence conservation policy and practice. Practical conservation efforts should pay special attention to these species because in situ conservation alone is ineffective as long as appropriate animal dispersers are absent from the habitat. Complimentary conservation measures should range from seed conservation programmes to the establishment of local nurseries propagating threatened species and the creation of ecological corridors. However, in the long term, reintroduction is only successful if the mechanisms of natural dispersal can be re-established, through the reintroduction of native dispersers, indefinite human intervention or the use of surrogate species (Pedrono et al., 2013).

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Data accessibility

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.dt940.

GBIF.org (7th February 2017) GBIF Occurrence Download http://doi.org/10.15468/dl.qmjrnj.

Authors' contributions

A. A.-D., S. B. and W. S. were involved in the research design; A. A.-D. performed the research and analysed the data; A. A.-D., G. E. O., S. P., R. R., F. R., O. H. R., H. S., K. V. and P. C. W. provided data; S. F. provided the R script to estimate Vb; all authors contributed to the writing of the manuscript.

Declaration of competing interest

The authors have no conflicts of interest to declare.

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